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Comparison of belowground biomass of natural deciduous forest and loblolly pine plantations

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With 6 figures

1. Introduction

1.1. General remarks

Knowledge of the dynamics of the aboveground component of forest biomass is extensive (Rodin and Bazilevich 1967), and current research has progressed to attempting to define forest biomass dynamics in terms of basic physiological processes underlying the accumulation of forest organic matter. Analysis of belowground biomass dynamics and the relationships to aboveground processes have been hindered largely by technical difficulties of measurement (Lieth 1968, Newbould 1967). Our concept of forest root biomass dynamics incorporates many untested assumptions because of the lack of satisfactory methods of study, and so parameter estimates are based on only a few data. As process-level research on forest metabolism has progressed, the role of roots in ecosystem function, and their energy demands associated with the accumulation and turnover of carbon and other essential elements, has been demonstrated as a vital link coupling physiological processes and their environmental constraints with total forest ecosystem behavior. For example, a preliminary synthesis of carbon metabolism of a temperate deciduous *(Liriodendron)* forest indicated that about 45% of the annual net carbon fixed was utilized in root respiration and biomass production belowground (Harris et al. 1972). Clearly, an annual carbon flux of this magnitude merits as a complete an interpretation as is possible of its significance in an ecosystem context.

1.2. Forest root biomass pools

Bazilevich and Rodin (1968) in summarizing the reserves of belowground organic matter in terrestrial ecosystems indicated that the broadleaved and subtropical forest types are characterized by a maximum of from 70,000 to 100,000 kg/ha of root organic matter (here defined as the total of living and recently dead root structure) which constitutes 15 to 33% of the total accumulated biomass. This belowground organic matter pool size is surpassed only by tropical forests; however, the proportion of the total biomass represented by roots is lowest for forests and ranges up to 90% for tundra and certain steppe vegetation types. Bazilevich and Rodin (1968) conclude from their review that, in general, the size of the root biomass pool is proportional to the total accumulated biomass, and as "site quality" decreases the proportion of total biomass as roots increases. Estimates of belowground biomass pools

have been obtained by soil monolith analysis (KARIZUMI 1968), allometric analysis (KIRA and OGAWA 1968), and only rarely by whole tree excavation. In addition to the extensive reviews by RODIN and BAZILEVICH (1967) and BAZILEVICH and RODIN (1968), extant data on root biomass pools have been summarized by OVINGTON (1962), BRAY (1963), and WHITT-AKER (1962).

1.3. Forest root biomass production

NEWBOULD (1967) states that no accurate figures have been obtained for belowground biomass production of forests, although much is known about root growth periodicity based on increases in length obtained from direct root observation. One approach commonly employed to estimate root production has been to assume that

$$\frac{\text{aboveground production}}{\text{aboveground biomass}} = K \frac{\text{belowground production}}{\text{belowground biomass}} \tag{1}$$

Because no data are available to establish values of K, the value of unity has been assumed. Thus unless otherwise specified, published estimates of forest root production have been determined from the assumption that above- and belowground relative production rates are equal.

Estimates of net belowground biomass pool size and net annual production of a tree can be estimated allometrically, but these provide only lower bounds for tree root production rates because seasonal mortality and biomass accumulation belowground are not included. KIRA and OGAWA (1968), for example, used the relationship

$$y = a\,x^b, \tag{2}$$

where y is a mass dimension (root), x is an independent dimension (e.g., aboveground biomass or stem diameter at breast height, dbh), and a and b are regression constants. The periodic increments to root and stem dimensions, $\triangle y$ and $\varDelta x$, can be incorporated as

$$y + \varDelta y = a(x + \varDelta x)^b, \tag{3}$$

and the resultant equation can be solved for root biomass increment. While this is an extremely useful technique for estimation of biomass pools and net annual production, here defined after NEWBOULD (1968) as $\varDelta$ biomass less mortality and consumption losses, the annual flux of biomass belowground cannot be estimated allometrically.

1.4. Objectives

In order to develop data bases for ecosystems and models for predicting ecosystem behavior based on component processes, an understanding of the dynamics of forest root biomass pools is needed. At intensively monitored terrestrial research sites in the Eastern Deciduous Forest Biome (EDFB) Program of the US-IBP, specific objectives of analyses of forest root biomass have been to determine: (1) belowground biomass pools and the size distribution of roots, (2) total annual root production, and (3) total annual root turnover through sloughing and herbivory.

2. Site descriptions and methods

2.1. Site descriptions

Analyses of belowground biomass in the EDFB Program have emphasized two types of forested ecosystems: natural deciduous forests and plantations of managed loblolly pine (*Pinus taeda* L.).

Natural deciduous forests typical of the Oak-Chestnut Forest Region (BRAUN 1950) of the Ridge and Valley Physiographic Province are being studied on the Energy Research and Development Administration Reservation at Oak Ridge, Tennessee. Forest types examined range from mesic hardwood associations of coves and valleys typified by the Liriodendron forest research area described by SOLLINS et al. (1973), through upland oak-hickory communities, to xeric oak-pine communities occupying ridge sites (Walker Branch Watershed being typical of the last two types). Soils are predominantly Fullerton and Bodine (typic paleudults). The climate of the Oak Ridge area has a mean annual rainfall of 139 cm and median annual temperatures averaging 14.5 °C (CURLIN and NELSON 1968).

Loblolly pine plantations, representing a large area formerly vegetated by mixed deciduous forests or abandoned farm land in the southeastern United States, are being investigated in the Piedmont area of North Carolina. The Saxapahaw research site occupies a 3.5 ha portion of a level bench overlooking the Haw River bottom. The area was machine-planted with trees in 1958 on a 2.5 × 2.5 m spacing. Soils are predominantly from the Granville series (typic hapludults). The area normally receives 116 cm of rainfall and has median annual temperatures averaging 15.5 °C.

2.2. Methods for deciduous forests

2.2.1. *Prefatory note*

Resources necessary to adequately study entire root systems of even a single dominant species size distribution represent a formidable investment. Deciduous forest belowground biomass and annual dynamics were therefore analyzed as a single compartment without regard for individual species composition. Operationally, three components were identified: (1) central stump root (ground level and below) and large support laterals to a radius of 60 cm from the stump perimeter, (2) coarse lateral root biomass (≥ 0.5 cm diam) at distances greater than 60 cm from any tree in the stand, and (3) roots < 0.5 cm diam. A combination of allometric analysis, soil block excavation, and monthly soil cores was used to obtain estimates of standing belowground pools and their annual dynamics.

2.2.2. *Stump biomass analysis*

An allometric equation was developed to estimate this component of belowground biomass from knowledge of dbh distribution. Trees tipped over in the course of constructing loading areas during local logging operations were cleaned, trimmed to dimension (central root and large laterals to a 60 cm radius), and weighed. Only trees that had been tipped over in the preceding six months were included in the sample; stumps showing any evidence of breakage were not included in the sample. Stumps were subsampled for determination of appropriate dry weight conversion. Large laterals were included to minimize bias associated with subsequent location of the limited number of soil blocks that could be excavated. The allometric estimator of the form $y = a x^b$ is based on multiple species (Table 1).

2.2.3. *Soil block analysis*

Lateral root biomass at distances > 60 cm from any tree (≥ 1.25 cm dbh) was estimated from a series of four replicate soil block excavations during July to August 1972 on each of 10 permanent forest plots on Walker Branch Watershed which were representative of both aboveground biomass (100,000 to 200,000 kg/ha) and dominant forest types of the area. Soil and root material were removed in 20 cm increments to a depth ≤ 60 cm, the extent of the major rooting zone. Subsequent backhoe excavations in the area to 3.5 m depth have substantiated this preliminary estimate of major root zone extent as do the results of KOCHENDERFER (1973). The area of the soil block varied with depth; the surface 20 cm portion was 0.56 m² (75×75 cm) while subsequent increments were 0.25 m² (50×50 cm). Roots were dry-sieved in the field; operations of washing and separation to size class were completed in the laboratory. Biomass of fine roots lost in dry-sieving was considered small. Roots were separated into the following diameter size classes: < 0.5, 0.5 to 1.0, 1.0 to 2.0, and > 2.0 cm. In order to analyze for covariance associated with distance and size of nearest trees, each pit analysis included measurement of distance to nearest trees in each of three diameter classes: 1.25 to 9.0 cm, 9.1 to 24.1 cm, and > 24.1 cm dbh.

Table 1. Summary of allometric relatioships developed to estimate belowground biomass components

Independent variable	Site	ln a	b	r	N	k*
Total root system weight (g); *Pinus taeda*	Triangle Area (North Carolina)	0.764	3.074	0.88	7	—
Central root + large laterals; mixed coniferous deciduous species +	Oak Ridge (Tennessee)	−2.3924	1.845	0.88	18	1.056

Equations are of the form $\ln \hat{y} = \ln a + b \cdot \ln x$, where $x = $ dbh (cm). [r is the correlation coefficient, and N is the number of sample.]

*) The constant "k" is a factor to correct the retransformation of $\ln \hat{y}$ for bias associated with geometric properties of the logarithmic transformation. The correction uses programs developed by BEAUCHAMP et al. (1973).

+) Species included in the sample were *Oxydendrum arboreum* L. (SOURWOOD), *Liriodendron tulipifera* L. [yellow poplar], *Pinus virginiana* MILL. [Virgina Pina], *Quercus alba* L. [white oak], *Q. prinus* L. [chestnut oak], *Q. rubra* L. [northern red oak] and *Prunus serotina* EHRH. [black cherry]; dbh of sample trees ranged from 7 to 28 cm.

2.2.4. *Analysis of seasonal dynamics*

The seasonal dynamics of lateral root biomass were determined in the Liriodendron forest research area. Sampling began in April 1971 and continued through March 1973. Sampling involved extracting one core (10 cm diam) in 15 cm increments to a 60 cm depth at each of 15 stations. The coring device consisted of a masonary hole saw cutting edge attached to a stainless steel cylinder with the shaft adapted to a gasoline-powered auger assembly. During the 1972 to 1973 period, sampling was conducted at approximately the same time as in the first year as well as during periods not included in 1971 in order to more clearly establish the annual pattern of belowground biomass. Soil material was washed from the roots over a 6 mm screen. The root material was divided into two diameter classes, < 0.5 cm and > 0.5 cm, dried (100 °C) following standard procedures, and weighed.

2.2.5. *Methods for loblolly pine plantations*

While generally similar to the field methods employed in analysis of uneven-aged natural deciduous forests, the relatively more uniform tree size and spacing characteristic of monospecific plantations simplified sampling. Seven entire root systems were harvested by excavating four 1 m³ volumes around each central root. Root material was separated into stump and lateral root components. Lateral root biomass was further separated into the following diameter size classes: < 0.1, 0.1 to 0.2, 0.21 to 0.5, 0.51 to 1.0, 1.01 to 2.5, 2.51 to 5.0, 5.01 to 10.0, and > 10.0 cm. An allometric relationship of total root weight to dbh was established (Table 1) and used to estimate belowground biomass.

2.2.6. *Analysis of seasonal dynamics*

Analysis of seasonal dynamics of lateral roots began in June 1972 and utilized a similar coring device (15 cm diam). Samples were collected at approximately monthly intervals to a depth of 20 cm with biomass estimates adjusted to a 70 cm depth based on the depth distribution determined from excavation of entire root systems. Soil-root cores were extracted systematically from points located on a coordinate grid within row spaces. Root material of < 1.0 cm diam was washed from the soil, dried, and weighed following standard procedures.

3. Results

3.1. Belowground biomass pools

Total belowground biomass pools ranged from 32,000 to 47,000 kg/ha for the deciduous and mixed coniferous-deciduous forest stands examined which had total aboveground biomass pools ranging from 110,000 to 185,000 kg/ha (Fig. 1). Aboveground biomass pools were estimated allometrically from dbh data and allometric equations reported elsewhere (HARRIS et al. 1971, HARRIS et al. 1973). The more mesic Liriodendron forest followed a pattern of biomass distribution similar to upland hardwood stands with a total aboveground biomass
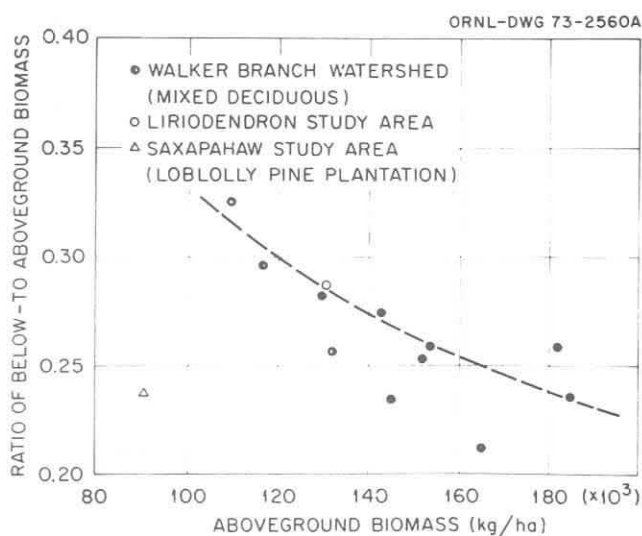

Fig. 1. Distribution of below- to aboveground biomass ratios over a range of aboveground biomass pool sizes on Walker Branch Watershed. The dashed line is a hand-fitted approximation of the trend noted by RODIN and BAZILEVICH (1965) for broadleaved deciduous forests. The displacement of the loblolly pine ratio appears to follow the trend for coniferous forests where ratios typically are lower.

Table 2. Percent composition of belowground biomass among stump and lateral root size class (diameter) components

Forest type	Percent composition				
	< 0.5 cm	0.5—1.0 cm	1.0—2.0 cm	> 2.0 cm	Stump[a]
Hardwood	21.0	7.8	7.0	9.3	54.9
Loblolly pine	13.4	6.6	2.7[b]	27.3[b]	50.0

a) Stump is defined differently for the forest types. The hardwood stump consists of the central root (belowground level) and laterals to a radius of 60 cm of the stump perimeter, while the loblolly pine stump consists only of the central root.

b) The diameter size classes for the loblolly data actually are 1.0—2.5 cm and > 2.5 cm.

of 130,000 kg/ha and a belowground biomass pool of 36,000 kg/ha. The loblolly pine forest deviated considerably from the pattern observed in deciduous forests. The total aboveground estimate, which was obtained by procedures reported elsewhere (RALSTON et al. 1972), was 90,000 kg/ha while belowground biomass amounted to 21,500 kg/ha.

3.2. Apportionment among stump and laterals

In the coniferous plantation and natural deciduous forests, 50% of the belowground biomass is represented by stump material (Table 2). The higher estimate of stump biomass (about 55%) obtained in analysis of deciduous forests is probably the result of including a portion of the lateral root biomass in the estimation procedure. A sharp contrast exists between coniferous plantations and natural deciduous stands in the proportion of belowground organic matter in the < 0.5 cm and > 2.5 cm diam size classes. The loblolly plantation had nearly twice the proportion of lateral root material in the > 2.5 cm size class, but in the hardwood forests the biomass in roots < 0.5 cm averaged nearly 1.5 times that of the loblolly pine plantation. These differences are a reflection of extreme types of root branching habits.

The contribution of lateral roots by size class was consistent among deciduous forest stands (Fig. 2) with the exception of > 1.0 cm diam roots. This variation probably reflects differences in overall stand density or the influence on the sample of trees neighboring any of the four root excavation pits in each stand.
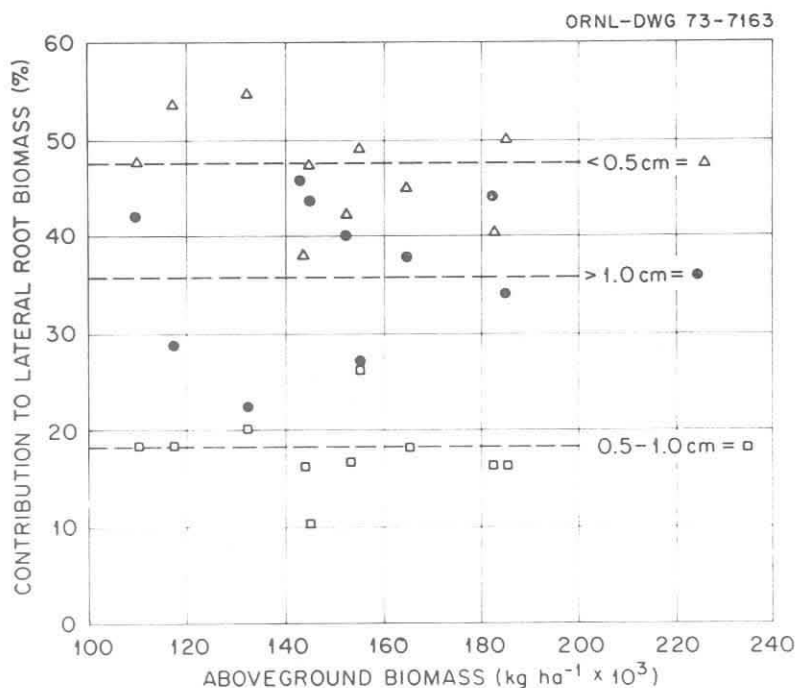

Fig. 2. Contribution of lateral root biomass by size classes (< 0.5 cm, 0.5 —1.0 cm, and > 1.0 cm) relative to the total pool of lateral roots (roots at distances > 60 cm from any tree > 1.25 cm dbh) for hardwood forests stands (Walker Branch Watershed) with aboveground biomass pools ranging from 110,000 to 185,000 kg/ha.

Table 3. Mean annual distribution of lateral root components with depth for a mesic *Liriodendron tulipifera* forest and a 15-year-old *Pinus taeda* plantation

Depth (cm)	*Liriodendron*, Size Class				Depth (cm)	*Pinus taeda*, Size Class			
	< 0.5 cm (kg/ha)	(%)	> 0.5 cm (kg/ha)	(%)		< 1 cm (kg/ha)	(%)	> 1 cm (kg/ha)	(%)
0—15	4810	63	3860	44	0—10	1980	46	2145	33
15—30	1680	22	3245	37	10—20	1075	25	2990	46
30—45	764	10	1490	17	20—30	430	10	715	11
40—60	380	5	175	2	30—40	390	9	520	8
					40—50	170	4	65	1
					50—60	130	3	30	0.5
					60—70	130	3	30	0.5

Values are mean annual pools of biomass and the percent found in each size class within the depth examined.

3.3. Root biomass distribution with depth

From 80 to 90% of the lateral root biomass was found in the upper 30 cm of the soil profile in both yellow poplar and loblolly pine forests (Table 3). Below 45 to 50 cm depth, the proportion of root biomass present decreased sharply. Backhoe excavations of the deep residual soils of Walker Branch Watershed revealed that root occurrence below 2.0 m was infrequent. Qualitative examination of the number of root endings on the deep pit faces suggests that root distribution from 60 to 100 cm is uniformly low. Below 100 cm, root occurrence is less frequent.
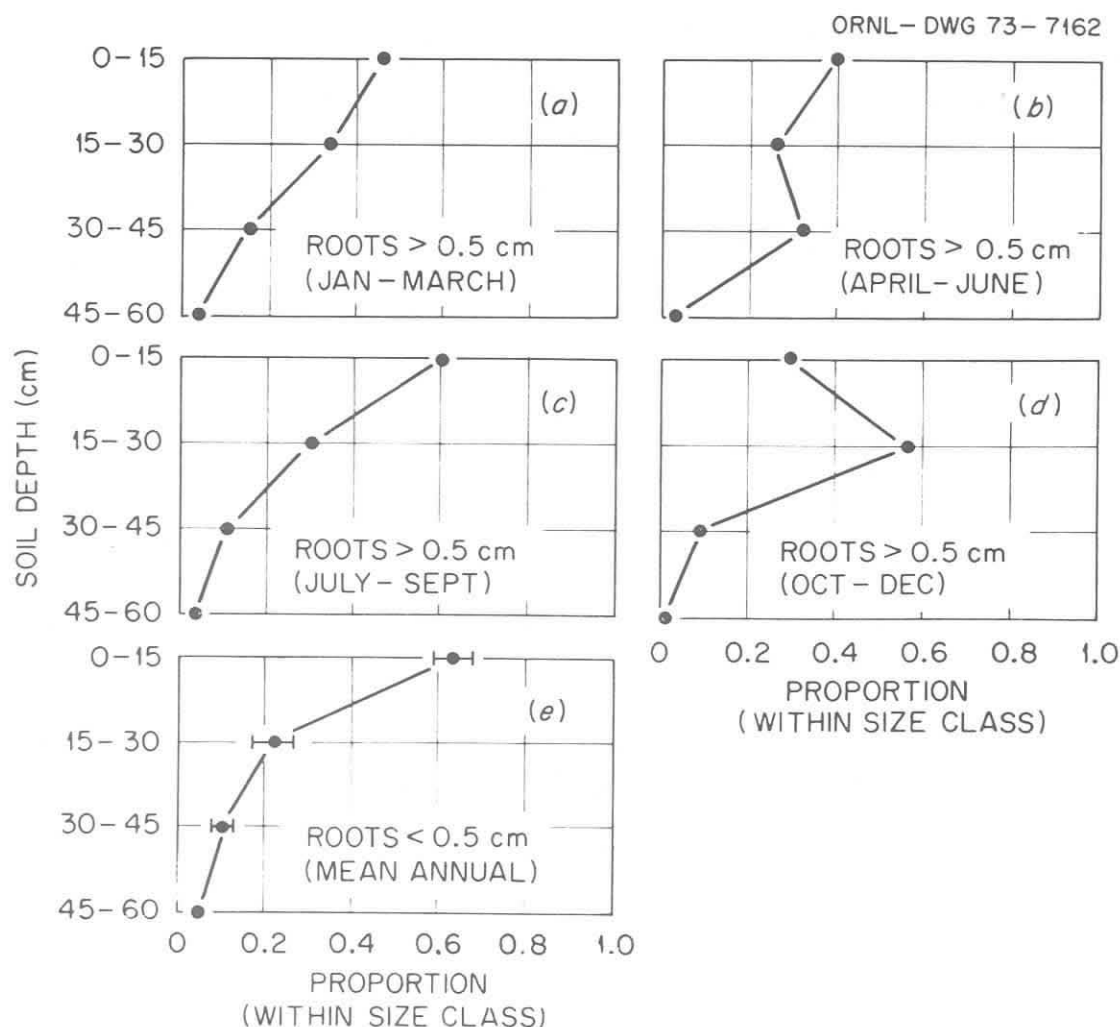

Fig. 3. Depth distribution in the *Liriodendron* forest of lateral roots expressed as a proportion of the total amount within each size class. The depth distribution of roots < 0.5 cm remained constant through the year as indicated by the range of values denoted by horizontal bars in e).

Periodic soil core collections from the Liriodendron forest were used to examine the seasonal variation of the depth distribution of roots within each size class (Fig. 3). Roots <0.5 cm maintained a similar biomass distribution with depth through the year even though biomass of roots <0.5 cm diam fluctuated two-fold. Roots ≥ 0.5 cm displayed considerable variation in depth distribution with little variation in biomass (Fig. 4). During April to June, roots ≥ 0.5 cm were equally distributed from 0 to 45 cm. During autumn, the larger proportion of this size class was found in the 15 to 30 cm zone, and only during summer and winter periods were roots ≥ 0.5 cm located primarily in the upper 15 cm zone. This pronounced temporal pattern of depth distribution suggests that for roots ≥ 0.5 cm the processes of biomass accumulation, translocation, and turnover occur differentially with depth during an annual cycle.

3.4. Annual net biomass production, turnover, and accumulation

The lateral biomass pools of both the yellow poplar and loblolly pine forests showed considerable variation in the smaller root size classes (Figs. 4 and 5). Small roots within deciduous forests are characterized by a peak in late winter (1 March), a minimum in mid-May, a second peak in mid-September, and a minimum in early winter (December to January). This pattern appears to be consistent among successive years. Based on summation of positive differences of seasonal trough and subsequent peak biomass estimates, net root biomass production was 9000 kg/ha, with a net annual turnover (translocation and sloughing) of equal magnitude. This value of net annual small root production is 2.8 times larger than mean annual aboveground wood production determined for the study area from allometric equations and periodic (1965 to 1970) dbh inventory (SOLLINS et al. 1973).
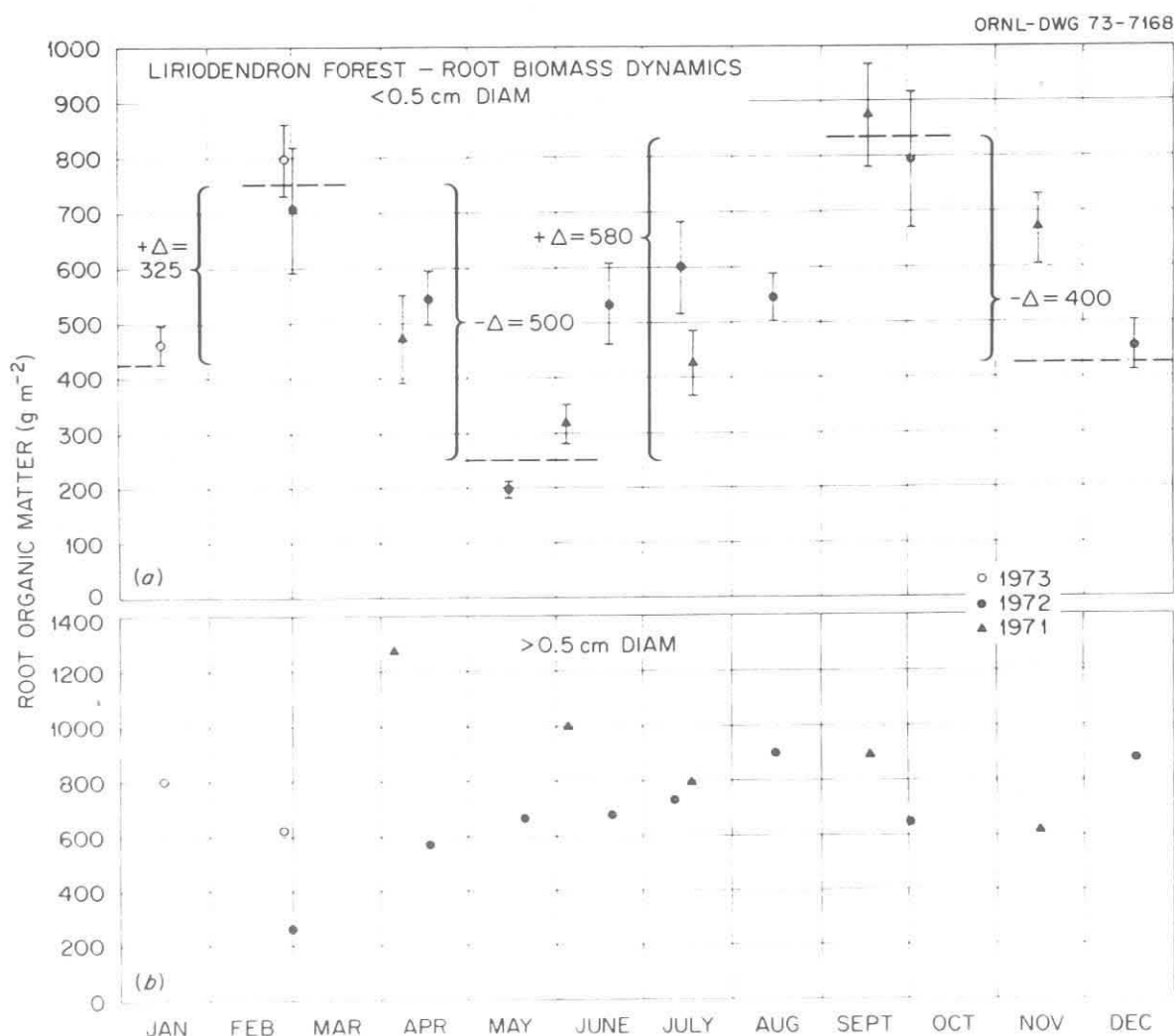

Fig. 4. Seasonal distribution of lateral root biomass in a Liriodendron forest for (a) roots <0.5 cm diam and (b) roots ≥0.5 cm diam ($\bar{x}$ ± 1 s.e.). Net biomass production and turnover were calculated from differences in pool size through the year. Based on monthly summary of core data, no consistent pattern of biomass dynamics could be detected for roots >0.5 cm diam.

Lateral root biomass ($<$ 1.0 cm diam) in the loblolly plantation exhibited minimum values in midsummer, early winter, and midspring (Fig. 5). Biomass peaks occurred in late autumn, late winter, and possibly late spring. Based on summation procedures, net root production amounted to 8600 kg/ha. Annual turnover was of similar magnitude to net production. Less than one year are available and so no conclusions can be reached concerning the year-to-year variation, but fluxes of belowground biomass appear to be at least similar to those observed in the Liriodendron forest.

4. Discussion

4.1. Ratio of below- to aboveground biomass

For both plantation and deciduous forest ecosystems, the ratio of below- to aboveground biomass (Fig. 1) followed trends similar to those reported by RODIN and BAZILEVICH (1967). They report that the percentage contribution of roots to total forest biomass of coniferous forest ecosystems approaches a constant value of 22.5 % as total biomass exceeds 75,000 kg/ha. Roots comprised 19 % of the total loblolly pine biomass. The proportion of biomass contributed by roots in deciduous forests approaches a constant value more slowly (RODIN and BAZILEVICH 1967). The proportion tends to stabilize at about 20 % as total biomass approaches 300,000 kg/ha. The root/shoot ratios of hardwood forests on Walker Branch Watershed follow the trend (dashed line, Fig. 1) suggested by the geographically more extensive data summary of RODIN and BAZILEVICH (1967). The pattern of below- to aboveground biomass distribution, which appears to be consistent over a wide range of forest types and local site variation, can be used to derive proportionality constants which describe (1) the size of the belowground biomass pool and (2) the net annual biomass production over some interval when estimates of aboveground biomass pool and accumulation are known. While useful as a means of indirectly estimating belowground biomass pool size and net annual production, this approach cannot be used to determine total annual root production.
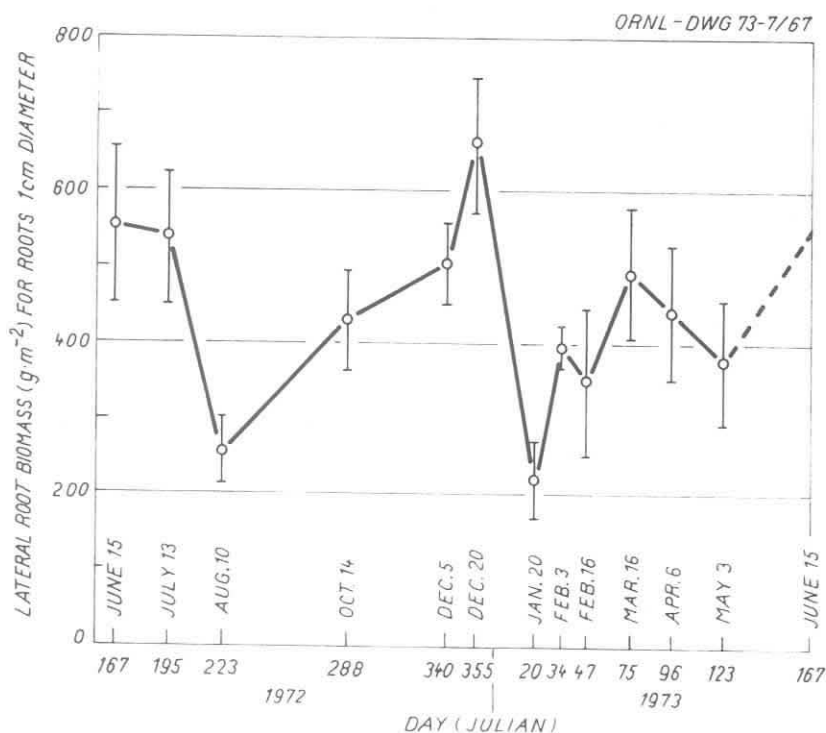

Fig. 5. Seasonal distribution of lateral root biomass ($<$ 1.0 cm diam) in a Pinus taeda plantation ($\bar{x}$ ± 1 s.e.). Net biomass production and turnover were calculated from differences in pool size through the year.

On an annual basis, root core analysis and other harvest techniques lack the precision to readily detect net annual belowground accumulation of biomass. However, applying the rather consistent values of below- to aboveground biomass ratios to stand data on biomass of tops would suggest that total belowground biomass pool should increase about 3 to 7% each year over the range of stand development examined.

4.2. Belowground biomass distribution among size classes and depths

The apparent constant apportionment of belowground biomass between stump and lateral components (Table 2) and the general constancy of allocation among lateral root size classes (Fig. 2) suggest that annual root biomass accumulation follows a systematic pattern over a several-year period of stand development (stand development here defined as biomass accumulation) for diverse deciduous forest types (xeric Pinus-Quercus to mesic Liriodendron forests). One mechanism that may influence the maintenance of a constant pattern of biomass distribution among lateral root size classes is the cyclic renewal of large structural roots. KOLESNIKOV (1968) has reported "root shedding" of large structural roots as well as the smaller sized laterals in orchards.

In the root pit excavations on Walker Branch Watershed, dead roots >2.5 cm diam, which were apparently associated with living overstory trees, were commonly observed. If such cyclic renewal of structural roots in forests is a common phenomenon, it represents a labile sink of organic matter and essential elements; the replacement of these roots represents a significant allocation of photosynthate even over a 100-year period. While of unknown extent and periodicity, the phenomenon of cyclic renewal of large structural roots could act as a long-term control mechanism, acting to stabilize biogeochemical cycles of forests through slow death and decay of root biomass.

Evaluations of site factors affecting productivity have often included edaphic variables. Measurements describing the "effective depth" of the soil profile have been found to be associated with site productivity by many investigators (HERMANN 1974, RALSTON 1964, Table 3). Any edaphic situation, such as claypans, hardpans, bedrock, or soil horizons of reduced permeability to air and water, limits rooting volume. One striking observation of interaction of root distribution and soil properties was the limiting effect of a relatively small change in B-horizon consistency (from firm to very firm) on root penetration. Depth of the A-horizon appears to have little influence on root distribution.

Based on the deep pit excavations, as well as observations by KOCHENDERFER (1973), restricting soil block excavations to the extent of the major rooting zone (upper 60 to 70 cm) will result in no more than a 5% underestimate of total belowground biomass. This biomass fraction, though small, may be physiologically important in water metabolism and element cycling. Recent studies of the Fullerton soil series (dominant on Walker Branch Watershed as well as much of the Ridge and Valley Province) indicate that there a few tree roots penetrate to the soil-bedrock interface the litter-soil calcium pools reflect calcium input from weathering of primary minerals.[1])

4.3. Biomass dynamics

Other experimental data on ecosystem carbon metabolism for the Liriodendron forest study area corroborate the existence of a large, annual belowground allocation of carbon. Estimated net photosynthetic influx and soil-litter carbon efflux yield an amount of unaccounted carbon input to soil equivalent to 7500 kg organic matter per ha (REICHLE et al. 1973, HARRIS et al. 1973, EDWARDS and SOLLINS 1973, DINGER 1972). For the same dominant species, Liriodendron tulipifera, ^{14}C-sb rose tracer field studies indicate a vernal allocation of root-associated labile carbon aboveground of approximately 1500 kg/ha organic matter.[2])

1) M. E. Springer, personal communication.

2) H. H. SHUGART and W. F. HARRIS, unpublished data.

Thus, for temperate deciduous forests, the assumption of a value of unity in Eq. (1) would lead to an underestimate of total annual root production. Our data for the Liriodendron forest indicate a more reasonable value of K to be 0.357 (1/2.8); this approximation incorporates the assumption that most of the root dynamics at an annual/seasonal scale are associated with roots <0.5 cm diam in deciduous forests or <1.0 cm diam in loblolly pine.

The present size of the root coring device and also the number of replicate cores that can be reasonably collected at each date restrict adequate characterization of the seasonal dynamics of roots >0.5 cm diam in the Liriodendron forest. The biomass pool appears to remain stable at 7000 to 9000 kg/ha (Fig. 4). Overall, the growing period of the belowground portion of the Liriodendron forest appears to start in early January. If root-core data are grouped in quarterly periods (January to March, April to June, July to September, and October to December) and biomass is calculated as the weighted average of variations infrequency distribution of individual core biomass estimates (≥0.5 cm only), an approximation of large lateral root biomass is possible (Fig. 6). This analysis suggests that the pool of roots ≥0.5 cm is at a minimum level during January to March, increases sharply during the spring and summer, and declines during autumn. The difference between fall and winter pool sizes of 800 kg/ha is well within the probable 3 to 7% annual increment inferred from knowledge of the below- to aboveground biomass ratio and annual aboveground biomass accumulation.
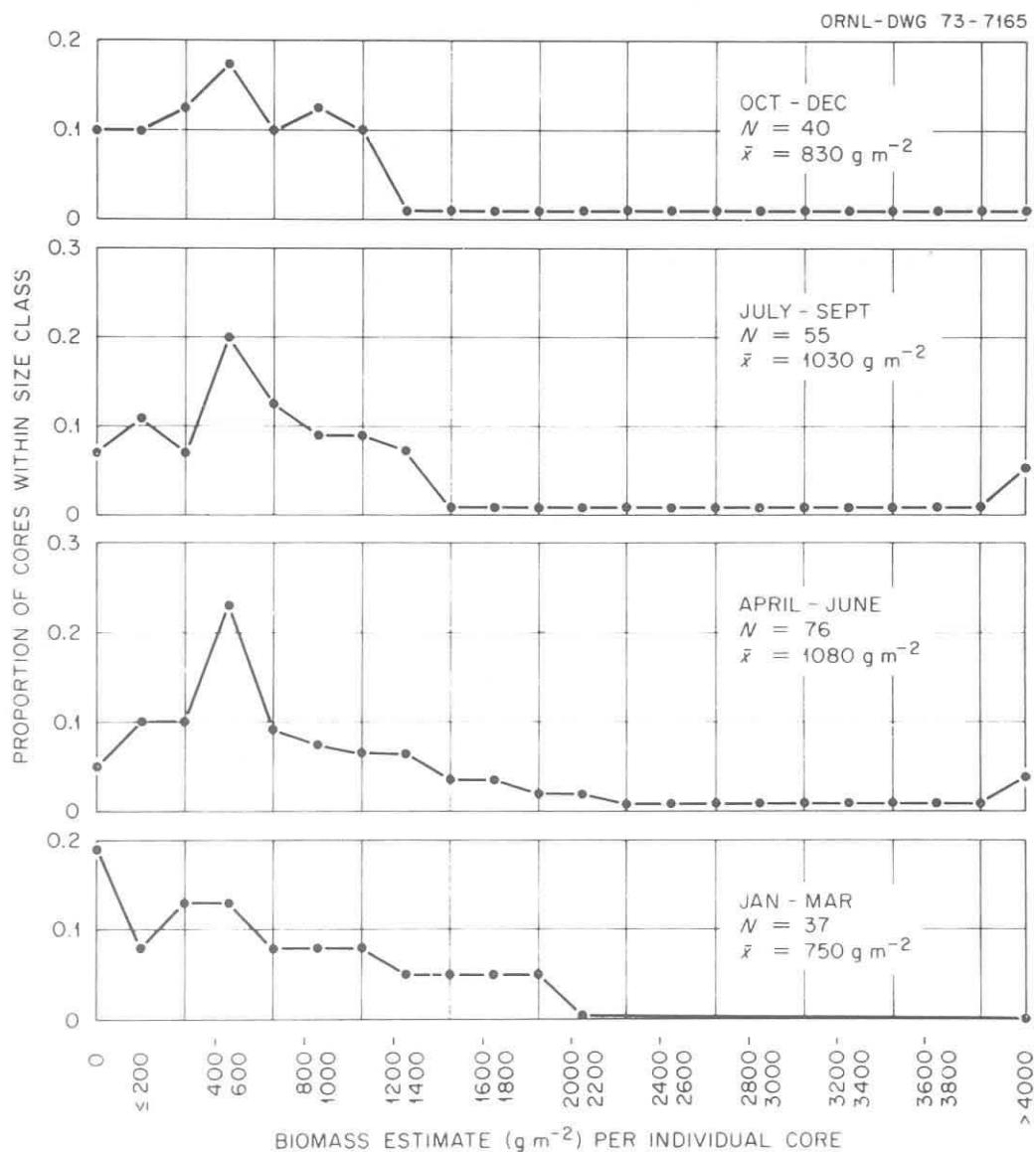

Fig. 6. Biomass distribution of roots ≥0.5 cm in a Liriodendron forest. By combining monthly samples over a three-month period some insight into the distribution and dynamics of the compartment can be gained. Biomass pools were calculated as the average weighted by the distribution of biomass estimates.

The major similarity between the coniferous and deciduous forest study sites is their similar temperate climate. Both forests exhibit considerable seasonal variation in root organic matter pools. Yet the root production/turnover results appear at variance with some other studies of root longevity using root observation chambers. Generally valid conclusions on the longevity of lateral roots, particularly those of small diameter, are difficult to formulate (LYR and HOFFMAN 1967). Reported longevity ranges from a few days (KINMAN 1932) to 10 years (HEIKURAINEN 1955). Our results suggest a longevity of about one year for small root size classes. However, considering the slower decay and shorter growing season associated with cooler climates, it seems unlikely that conclusions concerning root production/turnover can be generalized across broad climatic gradients without additional experimental evidence. Likewise, without additional evidence, generalization among taxonomic groups is tenuous. While the two species examined here are taxonomically dissimilar, they are both shade intolerant.

The large fluxes of belowground organic matter have implications for hypotheses concerning the strategies of forest ecosystems for resource allocation, and how these strategies might be interwoven with the coevolution of ecosystem components. The development of forest ecosystems that expend 50% of their annual photosynthate production belowground is probably not without selective advantage to the longterm survival of such a system. For example, how does energy expenditure belowground influence the tolerance of tree species to shading or other stresses which decrease production or the potential for production? Are large amounts of root turnover associated with all stages of the temperate forest sere or simply one portion (perhaps early in succession)? To what extent do root processes stabilize forest biogeochemical cycles and how have climatic regimes, soil processes, and properties operated in the natural selection processes leading to this apparent stability? And finally, to what degree are specific mycorrhizal associations responsible for root turnover and how do these associations influence the long-term survival of forest ecosystem types? Subsequent analyses of forest ecosystems must focus on these and related questions, if we expect fully to understand the theory underlying their structure and function.

Acknowledgements

5. Summary · Zusammenfassung

Analysis of the root biomass dynamics of deciduous and managed pine forests included the estimation of root biomass pools, the relationship to aboveground biomass pools which ranged from 100,000 to 200,000 kg/ha, and root size class distributions. Estimates of total root production for contrasting forest ecosystems were similar, about 9000 kg · ha^{-1} · yr^{-1}. These estimates of root production are 2.8 times greater than net annual wood production aboveground. Annual root turnover through sloughing and translocation was about 9000 kg · ha^{-1} · yr^{-1}. Most root activity was associated with roots < 0.5 cm diameter (deciduous forests) and roots < 1.0 cm diameter (loblolly pine plantations). Root longevity of these smaller roots appears to be no longer than one year.

Vergleich der unterirdischen Biomasse von natürlichen Laubwäldern und Kiefernforsten (Pinus taeda)

Analysen der Wurzel-Biomasse-Dynamik [des Wurzelmassenwechsels] von natürlichen Laubwäldern und Kiefernforsten schlossen die Schätzung des Wurzel-Biomassen-Pools, die Relation zum oberirdischen Biomassen-Pool (der zwischen 100 bis 200 kt/ha schwankt) und die Wurzel-Größenklassen-Verteilung ein. Die zur Unterscheidung (Kontrastierung) der Wald-Ökosysteme durchgeführten Schätzungen der totalen Wurzelproduktion glichen sich mit etwa 9 kt · ha^{-1} · a.$^{-1}$. Diese Schätzungen der Wurzelproduktion sind 2,8mal größer als die jährliche oberirdische Holz-Nettoproduktion. Der jährliche Wurzelmassenumsatz infolge des Absterbens [sloughing] und Abtrennung [translocation] von Wurzeln betrug etwa 9 kt · ha^{-1} · a.$^{-1}$. In Laubwäldern war die größte Wurzel-Aktivität bei Wurzeln der Größenklasse 0,5 mm ⌀ und in Kiefernforsten bei Wurzeln von 1,0 mm ⌀ festzustellen. Die Lebensdauer dieser kleineren Wurzeln scheint nicht länger als ein Jahr zu sein.

6. References

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